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Smallegange, I.M.; Coulson, T.

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The stochastic demography of two coexisting male morphs

ISABEL M. SMALLEGANGE1 AND TIM COULSON

Division of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY United Kingdom

Abstract. If genetically distinct morphs coexist under a range of natural conditions, they should have equal long-run fitnesses across a wide range of different stochastic environments. In other words, the sequence and frequency of good and bad environments should not substantially impact long-run growth rates. When different morphs have contrasting life histories that vary with environmental conditions, however, it seems improbable that growth rates can be equivalent across a range of stochastic environments without invoking a strong stabilizing mechanism to explain their persistence. As yet, there has been no research characterizing the long-run stochastic growth rate (\(\lambda_s\)) of different morphs across a wide range of stochastic environments. Assuming density independence, we show that the two genetic male morphs in the bulb mite (\(Rhizoglyphus robini\))—fighters, which are able to kill other mites, and benign scramblers—have similar \(\lambda_s\) in different Markovian environments (different simulated random sequences of good and bad habitats). Elasticity analyses revealed that \(\lambda_s\) was most sensitive to perturbation of adult survival rate. A slight (biologically and statistically realistic) increase in scrambler adult survival equalized scrambler and fighter \(\lambda_s\). The fitness equivalence of the two morphs suggests that stabilizing mechanisms, such as density or frequency dependence, required to maintain their coexistence, are weak. We advocate that stochastic demography can offer a powerful approach to identify and understand the circumstances under which genetic polymorphisms can be maintained in stochastic environments.

Key words: alternative reproductive phenotype; environmental variation; genetic male dimorphism; Markov chain; stage-structured population projection matrix.

INTRODUCTION

Identifying conditions for the coexistence of different genetic morphs within populations contributes to answering a key question in population biology: what maintains genetic diversity? Classical models in evolutionary theory state that for different genetic morphs to coexist, their mean fitness must be equal over time (Slatkin 1978, Gross 1996). This has been tested for natural populations, assuming constant environmental conditions (Shuster and Wade 1991). However, in nature, different populations of the same species likely experience different stochastic regimes (Tuljapurkar 1990). From these classical models (Slatkin 1978, Gross 1996) it follows that for coexistence to occur in different populations, the fitnesses of different morphs must be statistically indistinguishable in the long-run (although coexistence may occur only under certain sequences and frequencies of different environmental conditions). To our knowledge, there has been no research characterizing the long-run growth rates of different morphs across different stochastic environments. In density-independent stochastic environments, fitness in relation to vital rates such as survival and reproduction is measured by the long-run stochastic population growth rate (Cohen 1977, Tuljapurkar et al. 2003). Here, we test the hypothesis that genetically distinct morphs have statistically indistinguishable long-run stochastic growth rates across a range of stochastic environments. Long-term coexistence of morphs with statistically indistinguishable stochastic growth rates, however, likely requires stabilizing mechanisms such as density- or frequency-dependent selection (Gross 1996, Chesson 2000, Adler et al. 2007). Yet, the appropriate growth rate to use to describe outcomes in density- and frequency-dependent environments is context dependent (Metz et al. 1992, Metcalf and Pavard 2007), greatly complicating analyses of coexisting morphs. Therefore, for now, we resort to density-independent demographic models, which may under certain circumstances provide adequate approximations when density or frequency dependence operates (Caswell 2001).

The benefit of using density-independent, stochastic demographic methods is that it allows us to explore whether weak or strong stabilizing mechanisms are required for the maintenance and long-term coexistence of different, coexisting genetic morphs. Recent theoretical work shows that the strength of stabilizing mechanisms such as density or frequency dependence (Gross 1996) or a storage effect (Chesson 1994) depends on the degree of fitness equivalence (Chesson 2000, Adler et al. 2007). Specifically, if different genetic
morphs have similar stochastic growth rates, then coexistence can be maintained by weak stabilizing mechanisms (Chesson 2000, Adler et al. 2007), characterized by a near-zero slope of the relationship between fitness and relative frequency of each morph in the population (Adler et al. 2007). Yet, if large differences in stochastic growth rates exist between the different morphs, this would indicate that strong stabilizing mechanisms are needed to overcome the large fitness differences (Chesson 2000, Adler et al. 2007), and fitness functions are characterized by a negative slope of the relationship between fitness and relative frequency of each morph in the population (Adler et al. 2007). This novel demographic approach has obvious utility in understanding how environmental change could impact genetic diversity within polymorphic populations (Boyce et al. 2006). It may also inform on whether genetic diversity can be maintained through fluctuations in the stochasticity of the environment if the relative fitnesses of different genetic morphs vary with the color of environmental noise (so-called stochastic-environmental dependence).

We explore our premise for male bulb mites (Rhizoglyphus robini), which show two distinct morphs: heteromorphic males or “fighters” are armed with a thickened and sharply terminated third pair of legs which they can use to kill other males (Radwan et al. 2000), whereas homeomorphic males or “scramblers” have unmodified legs and are defenseless (see Plate 1). Apart from these morphological differences, the only other reported difference between the two morphs is that scramblers live longer than fighters (Radwan and Bogacz 2000). Why the two morphs coexist still puzzles biologists (Radwan 2007), mainly because scramblers always seem to be worse off as they, unlike fighters, are unable to kill rival males and monopolize access to females (Radwan et al. 2000, Radwan and Klimas 2001). The expression of male morph in the bulb mite is partially genetically determined (Radwan 1995). Here, we first aim to confirm that heritability of male morph is a general feature in the bulb mite. Because male morph expression can also depend on the environment (Radwan 1995), we also assess experimentally if this is the case for bulb mites in our experimental system. In the same experiment, we investigate the expression of a facultative dispersal morph (the hypopus) in relation to environmental quality and male morph. The experimental data, together with data from existing literature (Capua and Gerson 1983, Gerson et al. 1983, Radwan and Bogacz 2000) form the basis for constructing life tables for scramblers and fighters. From the life tables, we create a stochastic demographic model by constructing population projection matrices (PPMs) for fighters and scramblers living in two kinds of habitat: a high-food-quality and a low-food-quality habitat.

Using the stochastic demographic model we calculate stochastic growth rates of fighters and scramblers across a range of different stochastic environments, i.e., different sequences of good and bad habitats. In nature, bulb mites forage on high quality subterranean parts of plants such as bulbs and tubers (Diaz et al. 2000). Mite populations in high quality habitats rapidly increase in size, eventually utilizing the resource, upon which mites have to feed in low quality habitats until a new high quality habitat is discovered. Thus given that different populations of mites likely experience different environmental regimes, we might expect coexistence to be possible across a range of stochastic environments. By means of perturbation analysis we investigate the circumstances under which the stochastic growth rates of the coexisting male morphs are statistically indistinguishable.

**Methods**

**Heritability of male morph expression**

We set up fighter and scrambler lines (Appendix) and estimated heritability of male morph expression after five generations of selection using the so-called threshold model of quantitative genetics (Falconer 1989; Appendix). According to this model a continuously and normally distributed character, called liability, underlies the dimorphic variation, and the phenotypic expression of the variation is the result of a threshold. Individuals above the threshold develop into one morph, whereas individuals below the threshold develop into the other morph.

**Life tables**

The life cycle of the bulb mite consists of six stages (Fig. 1): egg, larva, protonymph, hypopus (also called deutonymph), tritonymph, and adult. The hypopus is a facultative dispersal stage to escape unfavorable environmental conditions and its development is induced by low food quality and quantity (Diaz et al. 2000). We constructed life tables for mites in a high-quality-food habitat (ad libitum access to yeast) and a low-quality-food habitat (ad libitum access to filter paper), which we will respectively refer to as the good and bad habitat.
Point estimates of fecundity and survival rates for females, fighters, and scramblers are available for the good habitat (Gerson et al. 1983, Radwan and Bogacz 2000), but not for mites living in the bad habitat (Table 1). To obtain estimates of these vital rates for adults in the bad habitat (we assumed that juvenile development of males and females does not differ), we conducted an experiment following the methods of Gerson et al. (1983). A hundred larvae from the stock cultures were put in individual 10 mm diameter glass tubes with ad libitum access to yeast. Upon maturation, 12 mating pairs where the male was a fighter and 12 mating pairs where the male was scrambler were formed and were each put in a 3-cm Petri dish and given ad libitum access to filter paper. Each couple remained together throughout life and survival and fecundity of males and females were recorded daily. Mites were kept in an incubator at a constant temperature of 27°C and >70% relative humidity.

In a second experiment we estimated the probability that a protonymph survives to grow into either a hypopus or directly into a tritonymph, and also tested if male morph expression (i.e., the proportion of male offspring that are scramblers) differed between mites that developed in the different habitats. A detailed description of the experimental methods is given in the Appendix. Briefly, eggs from each of 22 fighter mating pairs and from each of 22 scrambler mating pairs were put in Petri dishes with ad libitum access to yeast. Eggs from another 22 fighter mating pairs and 22 scrambler mating pairs were put in Petri dishes with ad libitum access to filter paper. Half of all dishes within each habitat treatment underwent a 24-h dry period. The experimental design therefore had three treatments: sire male morph (scrambler/fighter), habitat (good/bad), and dry period (yes/no). Each treatment combination was replicated 11 times. After mites developed into larvae, the offspring that are scramblers) differed between mites we had only counted the number of males, we multiplied this number by two to obtain a total population count of each Petri dish. Observed sex ratios did not differ from 1:1 (Gerson et al. 1983) so our measure is representative of the whole population.

To conform to the assumption of density independence implicit in our stochastic demographic model, mites were kept in individual tubes during different experimental stages. Furthermore, to exclude density-dependent effects through exploitation competition, a likely mechanism to give rise to density dependence in this species (Lesna et al. 1996), we provided mites with ad libitum access to food in all experiments. Finally, previous studies have not found evidence for density- or frequency-dependent effects on the relative survival or mating success of the two male morphs under constant environmental conditions (Radwan and Klimas 2001) such as those in our experiments, fulfilling the assumption of density independence.

### Stochastic demographic model

The long-run stochastic growth rate, $\lambda_s$, is calculated over a period of length $T$ by taking the exponent of

$$\log \lambda_s = \frac{1}{T} \sum_{t=0}^{T-1} r_t$$

with $r_t = \log (\sum_i p(i + 1)/\sum_i p(i))$ and $p(i)$ is the population vector at time $t$. The stochastic demographic model is $p(t + 1) = A(t)p(t)$ where $A(t)$ is a stage-classified PPM at time $t$ defined by a Markov chain of habitat transition probabilities (see below). To parameterize each PPM, we first estimated the probability of growing from stage $i$ to stage $i + 1$, $\gamma_i$, assuming that the probability of growing into the next stage depends on the age distribution within the current stage. Assuming furthermore that the population is stationary (See Appendix: Figs. A2 and A3) and that the age distribution within stages is stable:

$$\gamma_i = \left[ \frac{\sigma_i}{\sigma_T} T \right] \left[ \frac{\sigma_T}{\sigma_i} T^{-1} \right] / \left[ \frac{\sigma_T}{\sigma_i} \right]$$

where $T_i$ is the duration of stage $i$ (Table 2) and $\lambda$ is the population growth rate. The daily survival probability in stage $i$, $\sigma_i$, equals $e^{\mu t}$, where $t = 1$ day and $\mu$ is the

### Table 1. Conditions of the good and bad habitat in this study and previous studies of which we used the results to construct the survival and fecundity functions for mites in the good and bad habitat.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Juvenile stages</th>
<th>Adult stage</th>
<th>Good habitat</th>
<th>Bad habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>garlic, 27°C (1)</td>
<td>garlic, 27°C (1)</td>
<td>filter paper, 27°C (1, 3, 4)</td>
<td>filter paper, 27°C (4)</td>
</tr>
<tr>
<td>Males</td>
<td>garlic, 27°C (1)</td>
<td>yeast/wheat germ, 24°C (2)</td>
<td>filter paper, 27°C (1, 3, 4)</td>
<td>filter paper, 27°C (4)</td>
</tr>
</tbody>
</table>

**Notes:** Numbers in parentheses refer to references and are coded: (1) Gerson et al. (1983); (2) Radwan and Bogacz (2000); (3) Capua and Gerson (1983), and (4) life table experiments of this study. Gerson et al. (1983) present average stage durations, survival rates and fecundity curves (all without SEs); Radwan and Bogacz (2000) present survival plots for fighters and scramblers (without SEs); Capua and Gerson (1983) present average stage durations of hypopodes (without SEs).
constant force of mortality over each time step of one day (calculated by estimating the slope of the regression of log-transformed survival probability [d^{-1}] against age [d] using the survivorship functions [Appendix: Fig. A4; Caswell 2001]). Estimated daily survival probabilities are given in the Appendix. Estimating \( \gamma_i \) involves an iterative procedure where the entries into the PPM are calculated using an initial value of \( \lambda \). The eigenvalues of the PPM yield the second estimate of \( \lambda \), with which the parameters are estimated again, until \( \lambda \) converges to four decimal places.

In terms of the parameters \( \sigma_i \) and \( \gamma_i \), the probability of surviving and growing into the next stage \( (G_i) \) and the probability of surviving and remaining in the same stage \( (P_i) \) are \( G_i = \sigma_i \gamma_i \) and \( P_i = \sigma_i (1 - \gamma_i) \). The probability of mites developing from a protonymph into a hypopus is given by \( \beta \times G_3 \), and the proportion of individuals that grows from a protonymph directly into a tritonymph as \((1 - \beta) \times G_3 \). The resulting stage-classified PPM takes the following form:

\[
\begin{bmatrix}
P_1 & 0 & 0 & 0 & 0 & F_6 \\
G_1 & P_2 & 0 & 0 & 0 & 0 \\
0 & G_2 & P_3 & 0 & 0 & 0 \\
0 & 0 & \beta G_3 & P_4 & 0 & 0 \\
0 & 0 & (1 - \beta) G_3 & G_4 & P_5 & 0 \\
0 & 0 & 0 & 0 & G_5 & P_6
\end{bmatrix}
\]

The point estimate of vital rate \( F_6 \) for reproductive output was calculated using the stage-classified birthflow formulation (Caswell 2001) because egg-laying occurs continuously: \( F_6 = \sqrt{\frac{1}{2m}}(m_6 + \frac{1}{2}m_6) \), where \( m_6 \) is the average offspring production in the adult stage. Because growth of mite populations is limited by the lifetime reproductive output \( (R_0) \) of females, and not of males, we scaled male \( R_0 \) so that \( R_0 \) of fighters and scramblers equaled that of females (assuming no reproductive senescence). Because scramblers live longer than fighters (Radwan and Bogacz 2000), this means that the daily rate of reproduction, \( F_6 \), was lower for scramblers than for fighters. This normalization, however, did not result in equal growth rates of fighters and scramblers (see Results). The PPMs for scramblers and fighters in the good and bad habitat are given in the Appendix.

### Table 2. Average durations (days) of the different life stages of females, fighters, and scramblers.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Good habitat</th>
<th>Bad habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Fighters</td>
</tr>
<tr>
<td>1 Egg</td>
<td>3.60</td>
<td>3.60</td>
</tr>
<tr>
<td>2 Larva</td>
<td>3.00</td>
<td>3.00</td>
</tr>
<tr>
<td>3 Protonymph</td>
<td>2.80</td>
<td>2.80</td>
</tr>
<tr>
<td>4 Hypopus</td>
<td>2.60</td>
<td>2.60</td>
</tr>
<tr>
<td>5 Tritonymph</td>
<td>31.00</td>
<td>40.20</td>
</tr>
</tbody>
</table>

Notes: For references, see Table 1. Empty cells indicate that there are no observations for those cells.

### Habitat Markov chain

The habitat is in one of two states: good or bad. The probability distribution of habitat states at time \( t \) is described by a two-state Markov chain. If state 1 is the good habitat and state 2 is the bad habitat, the Markov chain transition matrix \( \mathbf{H} \) is

\[
\begin{bmatrix}
1 - p & p \\
p & 1 - p
\end{bmatrix}
\]

where \( p \) is the probability of switching habitats. The autocorrelation of the habitat Markov chain \((p = 1 - 2p)\), which shows the color of the environmental stochasticity, differs with different values of \( p \). For illustrative purposes and simplicity we set the probability of moving from the good to the bad habitat equal to the probability of moving from the bad to the good habitat. In the Appendix we extend the results of our analyses for unequal probabilities of switching habitats (Appendix: Fig. A7). By iterating \( \mathbf{H} \), a time series of length 100000 (with an initial transient length of 1000 discarded) was generated (shortening the length of this chain did not qualitatively affect our results (Appendix: Fig. A6)). This sequence determined the habitat state that the population of each morph experienced at each time step. Given the habitat state at time \( t \), \( A(t) \) is then filled using point estimates of the vital rates for that habitat. In that way a PPM is generated at each time (Tuljapurkar et al. 2003), which was stored with associated vectors of population structure and reproductive value for further analysis. Because in this specific case the probability of switching from the good to the bad habitat always equals the probability of switching from the bad to good habitat, the expected percentage of time spent in each habitat is 50%.

### Results

#### Heritability of male morph expression

Over five generations, the total selection differential (expressed in standard deviation units of liability) equaled 4.518 for scramblers and 1.237 for fighters (Appendix). The total response to selection over the total selection differential, i.e. the realized heritability, equaled for scramblers 1.872/4.518 = 0.41 (Appendix).
Hence the estimated heritability of the underlying liability for the scrambler morph was 41%. For fighters, the total response to selection differential equaled 0.347/1.237 = 0.30 (Appendix) giving an estimated heritability of the underlying liability for fighter morph of 30%. The change in the fraction of scramblers over the course of five generations of selecting for fighters or scramblers is given in the Appendix (Fig. A1).

**Adult survival and fecundity in the bad habitat**

Age-specific survivorship functions and age-specific fecundity functions (expressed per day) for males and females in the bad habitat are given in the Appendix (Fig. A4) along with the survival and fecundity functions for males and females in the good habitat observed by Gerson et al. (1983) and Radwan and Bogacz (2000). Average longevity of adult fighters was 20.0 ± 4.3 (mean ± SE) days and of adult scramblers 28.5 ± 5.3 days. This confirms previous results that scramblers live longer than fighters (Tables 1 and 2; Radwan and Bogacz 2000). The average, total lifetime egg production $R_0$ of females in the good habitat was 85.65 (Gerson et al. 1983) and in the bad habitat 3.25.

**Hypopus induction and environmental determination of male morph expression**

During this experiment, we did not observe hypopodes in mite populations in the good habitat. In the populations in the bad habitat 75 mites (including males and females) developed into a hypopus. The total number of males in the experiment was 1252 so that the overall probability that a mite would develop into a hypopus was estimated at (assuming a sex ratio of 1:1 [Gerson et al. 1983]): $75/(2 \times 1252) = 0.03$. We ran a generalized linear model with binomial errors to test the effect of male morph and dry period on the proportion of hypopodes in mite populations in the bad habitat. Neither male morph ($\hat{p} = 0.69$, $t = 1.69$, $P = 0.09$), dry period ($\hat{p} = 0.21$, $t = 0.54$, $P = 0.59$), nor the interaction ($\hat{p} = -0.64$, $t = -1.21$, $P = 0.23$) had a significant effect on the proportion of hypopodes. Of the 46 hypopodes that were individually isolated, 25 developed into females and 21 into fighters (all survived to become adults). None of the hypopodes developed into a scrambler. A three-way analysis of deviance with binomial errors revealed that neither sire male morph ($M; \hat{p} = -0.06$, $t = -0.10$, $P = 0.92$), dry period ($D; \hat{p} = -0.02$, $t = -0.05$, $P = 0.96$) nor habitat ($H; \hat{p} = -0.28$, $t = -0.57$, $P = 0.57$) affected the proportion of scramblers in the male population. None of the interactions were significant either ($M \times D; \hat{p} = 0.04$, $t = 0.06$, $P = 0.95$; $M \times H; \hat{p} = -0.47$, $t = -0.63$, $P = 0.53$; $D \times H; \hat{p} = -0.18$, $t = -0.28$, $P = 0.78$; $M \times D \times H; \hat{p} = 0.56$, $t = 0.61$, $P = 0.54$).

**Perturbation analysis**

The stochastic growth rate $\lambda_s$ of the expected population size was lower for scramblers than fighters (although not necessarily significantly lower given the large amount of variation in, for example, longevity), irrespective of the probability of switching habitats (Fig. 2A), implying ultimate domination of fighters. The dominant eigenvalue $\lambda_A$ of the mean (weighted arithmetic average) PPM of vital rates is equivalent to the commonly used asymptotic growth rate (Tuljapurkar et al. 2003). The difference (although not necessarily significant given the large amount of variation in, for example, longevity) between $\lambda_s$ and $\lambda_A$ was highest when the probability of switching habitats was lower than 0.3, implying that a long sequence of bad days is worse than occasionally occurring bad days (Fig. 2A). This region is associated with red noise where the autocorrelation of the habitat matrix is high and positive. Additionally, at very low values of $p$, $\lambda_s$ of fighters was lower than the $\lambda_A$ of scramblers, whereas the reverse was true for other values of $p$, implying that environmental variation can
be of crucial importance in concluding which morph would ultimately dominate in a population.

Next we explored the stochastic elasticity ($E_{ij}$) of $k$ to the perturbation of the vital rates of the different size classes, and the elasticity of $\lambda_\alpha$ with respect to the mean of each vital rate ($E_{ij}^{\text{mean}}$). The elasticity of $\lambda_\alpha$ with respect to the variance of each vital rate ($E_{ij}^{\text{var}}$) is the difference between $E_{ij}^{\text{mean}}$ and $E_{ij}^{\text{var}}$ and is not reported here. The methods that we use are such that if the mean of each vital rate is perturbed ($E_{ij}^{\text{mean}}$), there is no change in variance so that only changes in the mean value of vital rates contribute to $k$ (likewise, when the variance of each vital rate is perturbed ($E_{ij}^{\text{var}}$), there is no change in variance so that only changes in the mean value of vital rates contribute to $\lambda_\alpha$ (likewise, when the variance of each vital rate is perturbed ($E_{ij}^{\text{var}}$), there is no change in variance so that only changes in the mean value of vital rates contribute to $k$). Survival of adults made the largest contribution to $E_{ij}$, and its elasticity was higher for scramblers than for fighters (Fig. 2B). Survival of larvae, protonymphs, and tritonymphs made the next largest contributions to $E_{ij}$, followed by the contribution of survival of eggs to $E_{ij}^{\text{var}}$ (Fig. 2B). The latter elasticities were always slightly higher for fighters than for scramblers. The range of values of $E_{ij}$ to the survival of eggs, larvae, protonymphs, tritonymphs and adults was largest in the red noise region (low values of $p$; Fig. 2B). Elasticities of $\lambda_\alpha$ to the other vital rates were always lower than 0.05.

Comparing scrambler and fighter growth rates

The elasticity analyses revealed that the survival rate of adults ($P_6$) made the largest contribution to $k$. To compare scrambler and fighter growth rates we explored how variation in $P_6$ of scramblers would affect the difference in $k$ between scramblers and fighters. As scramblers live longer than fighters (Radwan and Bogacz 2000, this study), this sensitivity analysis may also inform on the possibility of a trade-off between increased longevity as a scrambler (but low fighting ability), and increased fighting ability as a fighter (but reduced longevity). We conducted this sensitivity analysis for three probabilities of switching habitats, which are representative of the color of the environmental stochasticity: $p = 0.1$ (red noise), $p = 0.5$ (white noise), and $p = 0.9$ (blue noise). Perturbing $P_6$ in the good habitat PPM of scramblers revealed that an increase in $P_6$ up until unity did not result in equal $\lambda_\alpha$ for scramblers and fighters, irrespective of the probability of switching habitats (Fig. 3A). Perturbing $P_6$ in the bad habitat PPM of scramblers showed that an increase in adult survival rate of scramblers by at least 5% (depending on the probability of switching habitats) resulted in an equal $\lambda_\alpha$ of scramblers and fighters (Fig. 3A).
The next largest contribution to $\lambda_s$ in the elasticity analyses was the survival rate of protonymphs ($P_3$). Again we investigated the relationship between variation in $P_3$ of scramblers and the difference in $\lambda_s$ between scrambler and fighters. Perturbing $P_3$ in the good habitat PPM showed that a 26% increase in $P_3$ resulted in an equal $\lambda_s$ between scramblers and fighters (Fig. 3C). In contrast, a 7% increase in $P_3$ in the bad habitat PPM resulted in an equal $\lambda_s$ of scramblers and fighters but only at $p = 0.1$ (Fig. 3C). At other values of $p$, $\lambda_s$ of scramblers always remained lower than $\lambda_s$ of fighters with increasing $P_3$. Perturbing the two vital rates $P_6$ and $P_3$ in each PPM by the same amount revealed that an increase by at least 2.6% and 4.7% for $P_6$ and $P_3$ respectively, was required for $\lambda_s$ of scramblers to be equal to $\lambda_s$ of fighters (Fig. 3B, D). Exploring each of these perturbations over the whole range of probabilities of switching habitats revealed that coexistence was restricted to certain colors of the environmental noise (Fig. 4).

Last, we assessed if any of the above perturbations of vital rates are biologically realistic. To this end we first increased average adult longevity by a biologically realistic amount, for example one standard error of the mean. This increased average adult longevity to 33.8 days in the bad habitat and to 52.0 days in the good habitat (Radwan and Bogacz 2000). The corresponding increase in $P_6$ was 2.8% and 3.1% (assuming that 50% of adults are alive after having been alive for half their longevity). In both cases the increase is higher than the 2.6% that is required for $\lambda_s$ of scramblers to be similar to
The difference in the stochastic growth rate ($\lambda$) between scramblers and fighters with increasing probability of switching habitats. The lines denoting $P_s$ (in black) show perturbation by $5\%$ in the bad habitat PPM of scramblers (solid line) and perturbation by $2.6\%$ in both PPMs of scramblers (dotted line). The lines denoting $P_3$ (in gray) show perturbation by $7\%$ in the bad habitat PPM of scramblers (solid line) and perturbation by $5\%$ in both PPMs of scramblers (dotted line). The horizontal dashed line denotes zero difference between the growth rate of scramblers and fighters.

$\lambda$ of fighters (Fig. 3B). For $P_s$, an increase is not likely to be mediated through an increase in the longevity of protonymphs, but rather through an increase in the daily survival probability of an individual ($\sigma$). However, $\sigma$ was already estimated at unity for scramblers in the good habitat. For scramblers in the bad habitat $\sigma$ was 0.97, allowing a maximal increase of 3\%. Increasing $\sigma$ by 3\% increased $P_3$ by 1.7\%, which is lower than the 4.7\% required for $\lambda_s$ of scramblers to be equal to $\lambda_f$ of fighters (Fig. 3D).

**Discussion**

The existence of genetic variance in species populations is one of the central issues in evolutionary biology. We explored conditions for coexistence of genetically distinct morphs and hypothesized that if such coexistence occurs in different types of stochastic environments, then the coexisting morphs should have statistically indistinguishable long-run stochastic growth rates. We explored this premise for a heritable trait of the acarid bulb mite, combining stochastic demography with life-history experiments. Especially in acarids we might expect coexistence to be possible across a range of stochastic environments given that different populations of mites likely experience different environmental regimes. We observed that the stochastic growth rates of two genetically distinct morphs that differ considerably in their life history were equivalent across a range of stochastic environmental regimes. Additionally, the perturbation analysis showed that, across a range of environments, characterized by different frequencies and sequences of good and bad environmental conditions, vital rates of mites do not need to vary much with changing frequency or density in order for coexistence to occur. Moreover, the change in vital rates required to increase the long-run growth rate of scramblers was within the 95\% confidence interval around the point estimates, hence this change could not have been statistically detected. These results suggest that the coexistence of the two morphs requires weak stabilization operating on the two morphs (Adler et al. 2007).

Overall, our results support applications of stochastic demographic models in environments that assume density or frequency dependence, illustrating that stochastic demography offers a powerful approach to identify and understand the circumstances under which genetic polymorphisms can be maintained in stochastic environments.

In the mite family Acaridae, male dimorphism (fighters, scramblers) exists in a number of species of at least three genera (*Sancassania*, *Rhizoglyphus*, *Schwiberia*; Woodring 1969). In some of these species the alternative reproductive phenotypes are genetically monomorphic and male morph expression is controlled by population density (Radwan 1993, 2001). Male morph expression in the bulb mite is partially genetically determined (Radwan 1995), and this is confirmed by our selection experiment. The threshold model is rooted in the science of human diseases where it is used to estimate heritability of susceptibility to disease (Falconer 1989); if liability (to catch a disease) is below a certain threshold the “normal” phenotype is expressed, whereas the “affected” phenotype is expressed if liability exceeds the threshold value. Heritability of liability is then calculated by comparing the “affected” population with the “normal” population (Falconer 1989). In our selection experiment we calculated the heritability of liability for both fighters and scramblers, where each was the “affected” phenotype with the other phenotype being “normal,” but assuming that the same liability and threshold underlies male morph expression. However, the response to selection in our experiment was asymmetrical with a higher estimated heritability in the scrambler lines. This could be a simple statistical artefact, although previous studies found a similar asymmetric response to selection (Radwan 1995, 2003) and attributed this to directional dominance for the alleles determining the fighter morph (Radwan 2003). We did not find evidence for an environmental influence on male morph expression. However, this could be due to low statistical power as, in the same experiment, we also did not find an effect of male sire morph on male morph expression. More work is required to understand the genetic architecture and environmental influence on male morph expression in bulb mites.

Why the two morphs coexist still puzzles biologists (Radwan 2007), mainly because scramblers always seem to be worse off. Unlike scramblers, fighters are able to attack and kill rival males (Radwan et al. 2000), and in small groups fighters are sometimes able to monopolize...
access to females (in 15% of cases observed [Radwan and Klimas 2001]). The fact that the long-run stochastic growth rates of fighters and scramblers were very similar across a wide range of stochastic environments suggests that only weak stabilizing mechanisms are required for their coexistence (Adler et al. 2007). This is supported by the fact that no experimental evidence of either strong density or frequency dependence has yet been found for bulb mites, at least in constant environments (Radwan and Klimas 2001). To unequivocally confirm if weak stabilization is required for the coexistence of these morphs in stochastic environments, as suggested by our experimental results, further experiments are required. These experiments should focus on testing the consequences of stabilization and fitness equivalence for coexistence of different genetic morphs as outlined by Adler et al. (2007). This might, however, be challenging given the fact that we found that the change in vital rates required to increase the long-run growth rate of scramblers was within the 95% confidence interval around the point estimates. A more mechanistic understanding of why the two different morphs exist would also prove useful. Current understanding is that the morphs are partly genetically determined (Radwan 1995; this study), but the exact mechanism of morph expression has not yet been identified. Apart from classical (weak) frequency dependence, the dimorphism could also be maintained through what we term stochastic-environment-dependent selection. We observed that the relative fitnesses of the two morphs varied with the color of environmental noise so that fluctuations in the stochasticity of the environment could maintain the male dimorphism. This might, however, require a storage effect whereby individuals of the currently disadvantageous genotype survive until the next favorable episode of environmental noise (cf. Chesson 1994, Ellner and Hairston 1994). Radwan (2007) suggested that scramblers are “making the best of a bad job,” but this assumes that fighter legs are costly to develop, that mites in poor condition refrain from developing fighter legs, and that male condition is heritable (Radwan 2007). None of these assumptions have been tested or verified (Radwan 2007). As yet, the only positive difference in a life-history trait between scramblers and fighters that has been found is that scramblers live longer than fighters (Radwan and Bogacz 2000). Interestingly, adult survival turned out to be the vital rate that played the dominant role in our investigation on the coexistence of two genetically distinct morphs in stochastic environments.

The stochastic growth rates of scramblers and fighters based on our point estimates of the vital rates revealed that, in the long-run, bulb mite populations would be dominated by fighters (because their stochastic growth rate was highest). Unfortunately, the studies from which we collected most of the life table data did not report errors around the parameter estimates so we could not conduct our analyses using distributions of vital rates. We did, however, know the error distribution of adult longevity. An increase in scrambler adult longevity within one standard error of the mean (and a corresponding increase in scrambler adult survival rate; the rate to which $\lambda_{\text{sc}}$ was most sensitive in perturbation analyses) was sufficient to equalize the stochastic growth rates of scramblers and fighters across different types of stochastic environments. In variable environments, increasing chances of survival at the expense of other vital rates could increase fitness, as risks are spread across uncertain environmental conditions. Metcalf and Koons (2007) indeed found for semelparous life-histories that allocation towards survival, even at the cost of reduced fecundity, is favored in more variable environments. This might play a role in the evolution of scrambler mites: their fecundity rate was estimated lower than that of fighters, but their adult survival rate was higher, as a result of which their stochastic growth rate was comparable to that of fighters. Even more so, a slight increase in scrambler longevity resulted in a higher stochastic growth rate of scramblers than fighters at high probabilities of switching habitats (Fig. 4).

In conclusion, the life tables of fighters and scramblers were constructed in a frequency- and density-independent environment. The magnitude of stabilizing mechanisms such as density or frequency dependence necessary to ensure long-term coexistence of these two morphs likely is small, as the stochastic growth rates were statistically indistinguishable under a wide variety of environmental conditions. Therefore, we advocate the application of stochastic demographic models to identify and understand problems such as the coexistence and maintenance of different genetic morphs in stochastic environments. Stochastic demographic theory has provided tools to study how environmental variability affects population growth and fitness (Boyce et al. 2006). Here we show how this first experimental application of stochastic demography using laboratory populations opens up more opportunities for stochastic demographic research (Smallegange and Coulson 2009). For example, hypotheses on the consequences of altering the temporal distribution of vital rates on the long-run stochastic growth rate could be experimentally tested, either by imposing different mortality regimes or by altering the environment. Such experiments may also inform on the consequences of temporal correlation of environmental variation on time to extinction (Inchausti and Halley 2003, Boyce et al. 2006, Benäım and Schreiber 2009). Finally, laboratory populations are ideal model systems to trial the importance of evolutionary analysis in stochastic demography and to push forward our understanding of eco-evolutionary dynamics in stochastic environments.

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**LITERATURE CITED**


**APPENDIX**

Experimental designs and population projection matrices (Ecological Archives E092-063-A1).